

Growth, reproductive development and yield of tomato (*Solanum lycopersicum* L.) genotypes under mild temperature elevation

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ABSTRACT

The increases in daily mean temperature can have negative impact on different agricultural crops. Tomato being one of the important horticultural crops in India is sensitive to temperature elevations. Although extreme temperature episodes lead to severe effects, even the mild temperature elevation, which is just above the optimal threshold, can considerably alter crop growth and development. However, no mechanistic studies have been conducted to understand the growth, reproductive development and yield response of popular tomato genotypes under mild temperature elevation (MTE). Hence, the effect of MTE on four selected tomato genotypes (*Solanum lycopersicum* L.) was examined in temperature gradient tunnel (TGT). The MTE led to reduction in in vitro pollen germination, number of fruits, fruit set percentage, fruit weight, number of leaves, number of branches, plant height, total dry matter accumulation and harvest index. Concurrently, number of trusses, number of flowers and flower abortion were increased. The results imply that, even the mild MTE can adversely affect the growth, development and yield of tomato. Based on the maintenance of harvest index and fruit weight per plant under MET, cv. Arka Vikas and advanced breeding line IIHR 2195 are found to be potential candidates with diverse genetic capability to include in breeding programs for developing temperature tolerant cultivars for future climatic conditions.

Keywords: Climate change; temperature gradient tunnel (TGT); pollen viability; fruit set; temperature tolerance; yield

1. Introduction

Climate change and variability with predicted increase in frequency of high temperature episodes would lead to warmer day and night temperatures. The temperature increase over the optimal can influence the plant growth, development and yield under such conditions. The global climate change models predict an increase of 2°C daily mean temperature between year 2046 and 2065 and 3.7°C by 2100 (IPCC, 2013). The day and night temperatures are one of the key factors among the different climatic variables, which have immense influence on physiological and biochemical processes, plant growth, development and yield of agricultural crops; and enormous number of studies in diverse agricultural crops have well documented the adverse impacts of increased day and night temperatures (groundnut: [*Arachis hypogaea* L.], Prasad *et al*, 2000; kidney bean: [*Phaseolus vulgaris* L.], Prasad *et al*, 2002; cotton: [*Gossypium hirsutum* L.], Snider *et al*, 2009; soybean: [*Glycine max* L. Merr], Djanaguiraman *et al*, 2013; tomato: [*Lycopersicon esculentum* Mill.], Laxman *et al*, 2013; 2014; coconut: [*Cocos nucifera* L.] Sunoj *et al*, 2014; rice [*Oryza sativa* L.], Bahuguna *et al*, 2015; maize: [*Zea mays* L.], Sunoj *et al*, 2016; sorghum: [*Sorghum bicolor* L. Moench], Sunoj *et al*, 2017; wheat [*Triticum aestivum* L.], Sun *et al*, 2018). There are several physiological and biochemical processes reported to be affected

with changes in the day and night temperatures viz., decreased gas exchange, chlorophyll fluorescence transients, thylakoid membrane damage, chlorophyll index, antioxidant scavenging capacity, carbohydrate and protein metabolism and increased nighttime leaf respiration. All these changes can lead to variation in yield attributes, reduction in growth and yield (Djanaguiraman *et al*, 2013; Narayanan *et al*, 2015; Sunoj *et al*, 2016; 2017; Sun *et al*, 2018).

Tomato is an important horticultural crop around the world; and India stands next to China with a distinction of world's second largest producer of tomato. The annual production of tomato during 2016-2017 in India was 20.7 Mt (NHB, 2017). However, the global studies predict a 10 to 40 % probable loss in crop production in India because of rise in temperature by the end of this century; and the possibility of production loss is higher in diverse crops viz., wheat, mustard, pea, onion, garlic, plantation crops and tomato (Aggarwal, 2003; Parry *et al*, 2004; Samra and Singh, 2004; IPCC 2013; Naresh Kumar *et al*, 2008; 2016). Currently, tomato producing agro-climatic regions of India is already facing the challenge of fluctuations in temperature conditions during tomato growing seasons similar to the other parts of the world (IPCC, 2013; Ayyogari *et al*, 2014). For tomato, the required optimum mean daily temperature ranges from 25-30°C at different growth stages; and this range of temperature are important for maintaining normal net assimilation rate (Laxman *et al*, 2013). At the same time, crossing the upper limit above optimum range (>30°C; supra-optimal temperature) can cause alterations in vital metabolic process required for the sustainable growth, development and yield (Sato *et al*, 2000; 2004; 2006; Rosenfeld *et al*, 2006; Islam, 2011; Alsamir *et al*, 2017). Studies revealed that, like other crops, in tomato, supra-optimal day and night temperatures adversely affect the morphological, physiological and biochemical traits (Camejo *et al*, 2005; Zhang *et al*, 2012; Laxman *et al*, 2013; 2014; Alsamir *et al*, 2017).

The earlier studies conducted to understand the effect of mild and higher temperature elevation on tomato growth, reproductive development and yield reveal that the magnitude of temperature effect varies according to the intensity of temperature (mild or high). In tomato, higher temperature elevation caused reduction in number of pollen production, pollen germination, fruit set, increase in flower abortion, decreased number of fruits and individual fruit weight (Sato *et al*, 2000; 2004; Islam, 2011). On the other hand, under mild temperature elevation, the number of flowers, pollen grain production and the biomass were not affected, but there was a significant reduction in number of fruit set, pollen viability and number of pollen grains released (Sato *et al*, 2006). However, limited attempts have been made to understand the response of tomato genotypes to mild temperature elevation. The evaluation of tomato genotypes to assess their sensitivity to supra-optimal temperature stresses is very important, as the tomato growing regions of India are encountering such conditions. We may face such situations in tomato growing regions in near future. It is also pertinent to quantify the threshold temperatures that can cause negative impacts on tomato yields for better crop management. And such attempts would also help to identify cultivars that can withstand supra-optimal temperatures. Hence, main objective of current study was the mechanistic understanding of mild temperature elevation on growth, reproductive development and yield of four selected tomato genotypes. We hypothesize that the genotypes have inherent resilience to withstand mild temperature elevation due to the genetic variability; and such genotypes could be employed for cultivation or for developing cultivars suitable for the areas which would be encountering mild to high temperature elevations.

2. Material and methods

2.1 Plant material and growth conditions

The study was carried out during the months of October 2011 to February 2012 in Temperature Gradient Tunnel (TGT) established at Indian Institute of Horticulture Research (ICAR-IIHR), Bangalore, Karnataka, India (13°7'N 77°29'E) located at an elevation of 890 m. The mean maximum temperature in summer is about 32.8°C and mean minimum temperature about 21.7°C and the average annual relative humidity of this area is about 64%. The four tomato genotypes viz., cv. Arka Vikas, cv. Arka Saurabh, RF4A and IIHR 2195 (CLN 2114 DCF1-2-16-8-2-17) used in the current study were selected on the basis of performance in different seasons and stress tolerance. Cultivar Arka Vikas, performs well in all seasons (kharif; rainy, rabi; winter and summer) and cv. Arka Saurabh, is suitable for two main growing seasons (kharif; rainy and rabi; winter) in India. The advanced breeding lines, RF4A and IIHR 2195 which

have shown tolerance to moisture and high temperature stresses, respectively were also included in the study. The seeds of four selected genotypes were sown in pro-trays with coco peat as the growing medium in the shade net nursery. Twenty five day old seedlings were transplanted to 20 L capacity plastic containers (one plant per container) filled with soil, farm yard manure (FYM) and sand in the ratio of 2:1:1 and allowed to recover from transplantation shock. One week after transplantation, the containers were shifted to the temperature gradient tunnel (TGT) with dimensions of 18 m length, 4.5m width and 3m height covered with polycarbonate sheet (transmittance: 85% Photosynthetic Active Radiation; PAR) for imposition of two temperature treatments. TGT is constructed to create a temperature gradient from one end to another end. The one end of the TGT is fixed with two fans and other end with cooling pad. One set of four genotypes was arranged towards the cooling pad side and another set towards the fan side for imposition of ambient (AT) and mild temperature elevation (MTE), respectively. In this study, temperature elevation of $\sim 2^{\circ}\text{C}$ (± 0.5) above the upper limit of optimum temperature range (30°C) considered as MTE. The area near the cooling pad side maintained an average temperature of $\sim 30^{\circ}\text{C}$ (± 0.5) and area near the fan side maintained an average temperature of $\sim 32.5^{\circ}\text{C}$ (± 0.5). The temperature inside the TGT was maintained by the operation of fan and cooling pad system. When the temperature inside TGT exceeded the set level, the fan automatically switched on to maintain the temperature gradient inside the TGT. The plants were uniformly maintained with established cultivation practices; and plant protection measures were taken as and when it was required. The gradient temperatures were maintained only during the daytime as the temperature elevation inside the TGT was driven by solar radiation.

2.2 Pollen viability and in vitro pollen germination

To determine the pollen viability and in vitro pollen germination under AT and MTE, pollen grains were collected from freshly opened flowers from first, second and third trusses of four tomato genotypes, which were tagged one day before pollen grain collection (Peet, 1996). The flowers were collected between 0900 and 0930 h and immediately placed in plastic bag with moist paper towel to maintain humidity and were immediately transported to laboratory. Hanging drop method (Sfakiotakis *et al*, 1972) was used to determine the pollen germination and viability. Pollen germination media used for cotton (Kakani *et al*, 2005) was modified, standardized and used for tomato pollen germination. The pollen germination media was prepared by dissolving sucrose (15 g), H_3BO_3 (15 mg), $\text{Ca}(\text{NO}_3)_4 \cdot 4\text{H}_2\text{O}$ (500 mg) and $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ (20 mg) in 100 mL deionized water; and the germination media was freshly prepared every day. One drop of germination media was placed on concave glass slide; and collected pollen grains were sprinkled on the media. Finally, glass slides were sealed with thin glass cover slips using petroleum jelly and incubated in BOD incubator (AUTOMAT SUPER 10, India) for 2 h at 30°C . After incubation, pollen grains were stained with Alexander dye (1:50 dilution using deionized water from stock solution) (Alexander, 1969). The stock solution of Alexander dye was prepared with mixing ethanol (95%; 10 mL), malachite green (1%; 5 mL prepared in 95% ethanol), acid fuchsine (15 mL), glycerol (25 mL), and phenol (5g); and the total volume was made up to 100 mL using deionized water. To determine germinated, viable (stained purple) and non-viable (stained green) pollen grains, observations were recorded from minimum of ten fields from single slide using projection microscope (LEITZ Neo- PROMAR, Ernst Leitz Ltd, Canada) with 25/0.55 magnification factor. Pollens were considered as germinated, if the length of the pollen tubes were greater than the diameter of the pollen grains (Sunoj *et al*, 2017).

2.3 Fruit volume

Fruit volume was measured by following the modified method of Bozokalfa and Kilic, (2010). Two glass beakers (500 mL and 250 mL), distilled water and weighing scale (SI 234, Denver instrument, Germany) were used to determine the fruit volume. The glass beaker (250 mL) with distilled water was placed inside another glass beaker (500 mL); and tomato was slowly immersed in water in first beaker (250 mL). The overflowing water was collected in 500 mL beaker, transferred to smaller beaker and weight was recorded. The fruit volume was calculated by converting 1g water as 1 cm^3 .

2.4 Plant morphology, yield and dry matter accumulation

Plant morphological observations viz., number of leaves, number of branches, plant height and dry matter accu-

mulation were recorded at the end of the experiment. The observations on flowering and fruit formation viz., number of trusses, number of flower, flower abortion (peduncles without flowers also assumed as aborted flower) and fruit set percentage were recorded from 40 days of transplanting at weekly intervals. The data on number of fruits per plant, fruit volume and total fruit weight per plant were also recorded. For quantification of total dry matter accumulation, the harvested plants were separated in to different plant parts (leaves, stem and root) and dried at 60°C till uniform weight was attained. The per cent harvest index was calculated from ratio of economic yield (total fruit dry weight) and biological yield (total plant dry weight; including the fruit dry weight).

2.5 Statistical analysis

The experiment was conducted with six biological replications per genotype for each temperature treatment under randomized block design (RBD). Statistical analysis of experimental data was conducted using generalized linear model (GLM) in SPSS (SPSS Inc. Ver.16, Chicago, USA). The Duncan multiple range test (DMRT) was performed to compare the means of each traits.

3. Result

Significant differences in various parameters were observed among the four tomato genotypes when exposed to MTE. Across the temperature treatments, reduction in pollen germination ($P<0.05$), number of fruits per plant ($P<0.05$), fruit set ($P<0.05$), fruit weight ($P<0.05$), number of leaves ($P<0.01$), number of branches ($P<0.01$), plant height ($P<0.01$), total dry matter accumulation ($P<0.01$) and harvest index ($P<0.01$) were observed under MTE as compared with AT. However, the fruit volume was not affected significantly. Number of trusses ($P<0.01$) and flower abortion ($P<0.05$) were higher under MTE. The pollen viability ($P<0.05$) and number of flowers ($P<0.01$) showed a mixed response. The magnitude of above responses under MTE in studied traits differed among the genotypes.

3.1 Vegetative development

Overall, the MTE caused significant reduction in vegetative growth; and variation in genotypic responses were observed (Table 1). The highest reduction in number of branches was observed in genotype, IIHR 2195 and cv. Arka Vikas and least in RF4A. On the other hand, there was an increase in number of branches in cv. Arka Saurabh. Even a similar response was observed in plant height, where highest reduction was noticed in cv. Arka Vikas and lowest in RF4A. While there was highest reduction in number of leaves in cv. Arka Vikas followed by cv. Arka Saurabh; and least reduction in IIHR 2195 (Table 1).

Genotypes (G)	No. Of branches per plant		Plant height (cm)		No. Of leaf per plant	
	Treatments (T)					
	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE
RF4A	13 ^b	09 ^a (-31)	73 ^b	67 ^c (-8.2)	101 ^{ab}	80 ^a (-21)
Arka Saurabh	08 ^c	09 ^a (+13)	68 ^{bc}	60 ^c (-12)	67 ^c	46 ^c (-31)
IIHR 2195	15 ^a	10 ^a (-33)	100 ^a	90 ^a (-10)	73 ^c	60 ^b (-18)
Arka Vikas	15 ^a	10 ^a (-33)	85 ^b	62 ^c (-27)	116 ^a	53 ^b (-54)
LSD						
T		1.78**		3.98**		6.98**
G		1.88*		4.47*		8.34*
TxG		3.76*		8.94*		9.32*

Table 1. Number of branches, plant height and number of leaves in tomato genotypes grown at two temperature regimes AT: Ambient temperature; MTE: Mild temperature elevation; ** Significant at $P<0.01$, * significant at $P<0.05$; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test; Values in parenthesis indicate the percentage (%) increase (+) or decrease (-) over ambient temperature condition.

3.2 Number of trusses, flowers and flower abortion

The significant genotypic variations were observed in the number of trusses, number of flowers and flower abortion (Table 2). Across the genotypes, significant increase in number of trusses was observed under MTE. However,

among the genotypes, increase in number of trusses were higher in cv. Arka Vikas, while it was lowest in cv. Arka Saurabh when exposed to MTE as compared to plants grown at AT. With respect to number of flowers, mixed response was observed among the four genotypes tested. There was an increase in number of flowers in two genotypes, highest in IIHR 2195 followed by cv. Arka Vikas, while there was a reduction in number of flowers in RF4A and cv. Arka Saurabh. The MTE caused increased flowers abortion among all the four genotypes, with highest in IIHR 2195; and lowest in cv. Arka Vikas (Table 2).

Genotypes (G)	No. of trusses per plant		No. of Flowers per plant		Flower abortion per plant (%)	
	Treatments (T)					
	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE
RF4A	48 ^a	61 ^a (+25) ⁽	185 ^a	172 ^b (-7.0)	43 ^b	61 ^b (+43)
Arka Saurabh	22 ^c	24 ^c (+6.0)	85 ^d	80 ^d (-6.0)	41 ^b	54 ^c (+31)
IIHR 2195	27 ^{bc}	44 ^b (+63)	148 ^b	233 ^a (+57)	31 ^c	63 ^b (+102)
Arka Vikas	37 ^b	64 ^a (+71)	170 ^a	182 ^b (+7.0)	60 ^a	70 ^a (+16)
LSD						
T		7.078**		20.72**		3.4*
G		7.91**		23.17**		12.13*
TxG		15.82*		46.03*		21.02*

Table 2. Number of trusses, number of flowers and flower abortion in tomato genotypes grown at two temperature regimes

AT: Ambient temperature; MTE: Mild temperature elevation; ** Significant at P<0.01, * significant at P<0.05; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test; Values in parenthesis indicate the percentage (%) increase (+) or decrease (-) over ambient temperature condition.

3.3 Pollen viability, in vitro pollen germination and fruiting characteristics

Among the genotypes, increased pollen viability was observed in cv. Arka Vikas followed by cv. Arka Saurabh, while the other genotypes RF4A and IIHR 2195 showed slight reduction. However, on the other hand, the reduction in in vitro pollen germination was found across all the four genotypes, with highest reduction in RF4A and least in IIHR 2195 (Table 3). Consequently, the reduction in percent fruit set and number of fruits per plant were observed. The highest reductions in fruit set were observed in IIHR 2195 and lowest in cv. Arka Saurabh followed by cv. Arka Vikas. While lowest reduction in number of fruits were noticed in cv. Arka Vikas. At the same time, highest reduction in fruit weight was recorded in cv. Arka Vikas, while the least reduction was observed in IIHR 2195. On the other hand, highest increase in fruit volume was observed in cv. Arka Vikas followed by RF4A. However, the reduction in fruit volume was observed in IIHR 2195. No change in fruit volume was observed in cv. Arka Saurabh (Table 4).

Genotypes (G)	Pollen viability (%)		Pollen germination (%)	
	Treatments (T)			
	AT	+2°C MTE	AT	+2°C MTE
RF4A	58.5 ^a	55.5 ^c (-5.0)	37.8 ^c	12.7 ^d (-66)
Arka Saurabh	46.3 ^b	63.3 ^b (+37)	48.9 ^b	22.5 ^b (-54)
IIHR 2195	30.8 ^c	30.0 ^d (-3.0)	58.3 ^a	37.2 ^a (-36)
Arka Vikas	49.0 ^b	73.3 ^a (+50)	35.6 ^c	16.7 ^c (-53)
LSD				
T		11.66*		12.5*
G		5.05*		6.78*
TxG		26.08*		23.45*

Table 3. Pollen viability and pollen germination in tomato genotypes grown at two temperature regimes

AT: Ambient temperature; MTE: Mild temperature elevation; ** Significant at P<0.01, * significant at P<0.05; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test; Values in parenthesis indicate the per cent increase (+) or decrease (-) over ambient temperature condition.

Genotypes (G)	No. of fruit per plant		Fruit set per plant (%)		Fruit weight per plant (g)		Fruit Volume (cm ³)	
	Treatments (T)							
	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE
RF4A	97 ^b	82 ^a (-15) [†]	57 ^b	39 ^c (-32)	1938 ^c	1350 ^c (-30)	31.7 ^c	32.5 ^c (+3.0)
Arka Saurabh	65 ^d	38 ^b (-42)	59 ^b	46 ^b (-21)	2995 ^b	1827 ^b (-39)	55.0 ^a	55.0 ^a (0)
IIHR 2195	167 ^a	83 ^a (-50)	69 ^a	37 ^c (-46)	1689 ^d	1583 ^c (-6.0)	17.7 ^e	12.8 ^d (-27)
Arka Vikas	100 ^b	87 ^a (-13)	40 ^c	30 ^d (-25)	1960 ^c	1086 ^d (-45)	21.7 ^d	33.0 ^c (+52)
LSD								
T		11.66*		12.5*		274.37*		NS
G		5.05*		6.78*		354.21*		3.31**
TxG		26.08*		23.45*		NS		4.69**

Table 4. Number of fruits, fruit set, fruit weight and fruit volume of tomato genotypes grown at two temperature regimes AT: Ambient temperature; MTE: Mild temperature elevation; ** Significant at P<0.01, * significant at P<0.05, NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test; [†]Values in parenthesis indicate the percentage (%) increase (+) or decrease (-) over ambient temperature condition.

3.4 Dry matter accumulation and harvest index

The dry matter accumulation in leaf, shoot, root, fruits and overall total dry matter accumulation were reduced due to imposition of MTE in the tomato genotypes. The harvest index reduced in three genotypes except in cv. Arka Vikas which showed an increase. Compared to other genotypes, in cv. Arka Vikas, the reduction in leaf, shoot and root dry weights were higher and reduction in fruit dry weight. Due to which cv. Arka Vikas showed a slightly higher harvest index after the exposure to MTE (Table 5). While comparing the individual plant parts (leaf, shoot, root and fruit), the extent of reduction was different across the four genotypes. Reduction in fruit dry weight was higher in IIHR 2195 and lower in cv. Arka Vikas. The reduction in total dry matter accumulation was highest in IIHR 2195, while it was least in cv. Arka Saurabh. At the same time, highest reduction in harvest index was observed in IIHR 2195 and RF4A; and least in cv. Arka Saurabh.

Genotypes (G)	Dry matter accumulation (g/ plant)											
	Leaf		Shoot		Root		Fruit		Total		Harvest index	
	Treatments (T)											
	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE	AT	+2°C MTE
RF4A	111.4 ^a	80.6 ^{ab} (-28)	62.9 ^b	60.4 ^a (-4.0)	42.4 ^a	29.7 ^a (-30)	185.7 ^{ab}	97.2 ^a (-48)	402.3 ^{ab}	267.9 ^a (-33)	46.2 ^a	36.5 ^b (-21)
Arka Saurabh	72.6 ^{ab}	61.4 ^b (-15)	37.9 ^c	33.7 ^b (-11)	23.2 ^b	17.7 ^c (-24)	157.4 ^{ab}	93.3 ^a (-41)	291.0 ^{bc}	206.1 ^b (-29)	53.8 ^a	45.2 ^a (-16)
IIHR 2195	42.4 ^b	31.8 ^c (-25)	37.5 ^c	28.5 ^b (-24)	19.1 ^b	16.6 ^c (-13)	132.4 ^b	63.3 ^b (-52)	231.4 ^c	140.3 ^c (-39)	57.4 ^a	45.1 ^a (-21)
Arka Vikas	126.0 ^a	77.4 ^b (-39)	96.0 ^a	52.7 (-45)	42.1 ^a	23.0 ^b (-45)	126.5 ^b	91.3 ^a (-28)	390.7 ^{ab}	244.6 ^{ab} (-37)	32.5 ^b	36.4 ^b (+12)
LSD												
T		13.7**		12.6**		6.8**		38.3**		51.9**		7.1**
G		29.6**		19.9**		10.8**		44.2*		82.1**		11.2**
TxG		41.9**		20.6*		NS		NS		NS		NS

Table 5. Dry matter accumulation and harvest index in tomato genotypes grown at two temperature regimes AT: Ambient temperature; MTE: Mild temperature elevation; ** Significant at P<0.01, * significant at P<0.05, NS: non-significant; Means followed by the same letter in a column do not differ significantly according to Duncan's multiple range test; [†]Values in parenthesis indicate the percentage (%) increase (+) or decrease (-) over ambient temperature condition.

4. Discussion

The mechanistic evaluation of four tomato genotypes revealed that MTE can bring changes in vegetative growth, reproductive development, fruit development and total dry matter accumulation and harvest index. In general, earlier studies on effect of elevated temperature on different tomato genotypes also have reported the changes in growth traits, reproductive development and yield; and demonstrated the major role of genetic diversity in differential responses of diverse genotypes, which are similar to the findings of current study (Abdelmageed and Gruda, 2009; Alsamir *et al*, 2017). At the same time, studies on effect of MTE on growth, development and yield response of tomato genotypes are limited, except Sato *et al*, (2006); where the temperature used for the study was 32°C/22°C (day and night temperature). In their study, MTE did not significantly cause changes in biomass, number of flowers and the number of pollen grains produced. Although they observed a significant reduction in number of fruit set, pollen viability and number of pollen grains released. In the our study, the responses of four genotypes are conflicting with the findings of Sato *et al*, (2006), as we observed the effect of MTE on both vegetative and reproductive development consequently leading to yield reduction; and this diverse response can be the result of genotypic differences.

In the current study, reduction in vegetative growth can be attributed to the reduced photosynthesis rate, thereby causing reduction in overall growth of tomato genotypes under MTE. The reduction in photosynthesis rates of same four tomato genotypes used in current study was observed under MTE (Laxman *et al*, 2013); and the same trend was also observed in different agricultural crops under elevated temperature such as sorghum (Sunoj *et al*, 2017) and wheat (Sun *et al*, 2018). Further, variations in day and night temperatures can make the changes in leaf nighttime respiration, which in turn results in altered carbohydrate metabolism leading to reduced total dry matter accumulation (Sunoj *et al*, 2016). The changes in carbohydrate metabolism also plays an important role in reproductive development, which include flowering traits and microsporogenesis; and observed fluctuations in carbohydrate metabolism in the four tomato genotypes in our earlier study under MET can be the reason for changes in flowering traits in this experiment (Laxman *et al*, 2013). Even though, the flowering traits viz., number of trusses and flowers increased in current study, the higher flower abortions resulted in reduced number of fruits. The increased flower abortion under MTE is an indication of disturbed source sink relationship due to stress on carbohydrate metabolism, which can adversely affect the temperature tolerance in tomato genotypes (Sato *et al*, 2004; 2006). The sensitivity of reproductive development (flowering traits and microsporogenesis) to high and mild temperature stress are reported in several crops (groundnut; Prasad *et al*, 2000, cotton; Kakani *et al*, 2005, tomato; Sato *et al*, 2006, sorghum: Sunoj *et al*, 2017). At the same time, other studies on effect of temperature on tomato genotypes, also showed mixed response in flowering traits, such as no change, increase or reduction; and this inconsistency in results again points towards the differential response attributed to genetic diversity of tomato genotypes (Peterson and Taber, 1991; Wang *et al*, 2003; Sato *et al*, 2000; 2004; Firon *et al*, 2006; Abdelmageed and Gruda, 2009; Alsamir *et al*, 2017).

Starch is the major form of reserve in pollen grains; and a cascade of metabolic reactions is involved for the accumulation of starch in pollen grains. Disturbances in any point of starch synthesis pathway, altered sucrose hydrolysis and proline transport can lead to reduced pollen viability thereby resulting in decreased fruit set in tomato under MTE. The variation in total sugars, reducing sugars and proline in leaf tissues were reported in same genotypes in our earlier experiment and occurrence of these variations in sugars and proline can be the cause for changes in pollen viability and in vitro pollen germination in current study (Sato *et al*, 2006; Laxman *et al*, 2013). Further, earlier studies in tomato showed a positive correlation among the number of fruits, fruit set, pollen viability, release and germination (Firon *et al*, 2006; Sato *et al*, 2006). In our study, there were similar positive correlations found between pollen viability and fruit set as documented in the previous studies (Data not shown). Conversely, there was no correlation found between pollen viability, in vitro pollen germination, fruit set, number of fruits and final yield; and similar trend was observed on twenty four sorghum genotypes grown under high temperature at field condition (Sunoj *et al*, 2017). This indicates the partial contribution of pollen viability and germination; and inevitable importance of stigma receptivity for the reproduc-

tive success under elevated temperature conditions, which was not taken in account for current and previous studies in tomato. There are different important steps involved in the fertilization viz., pollen adhesion, hydration, polarization, germination and pollen tube invasion, which require active involvement of stigma; and a single viable pollen is sufficient for fertilization, that gives stigma receptivity equal importance as capability of pollen (Edlund *et al.*, 2004; Sunoj *et al.*, 2017). Tampering of any of the above fertilization steps either by incapability of pollen or stigma can lead to reduction in reproductive success and yield. Additionally, results also indicates that, the contribution of pollen and stigma for the successful fertilization varies with the genetic differences in the tomato genotypes that makes them perform differently in different seasons and geographic conditions, which is evident from the results of current study and supported by the findings of Sunoj *et al.*, (2017). Furthermore, lack of above correlation between pollen traits and final yield also can happen due to the failure of young fruits to reach maturity under MET. For the instance, cv. Arka Vikas showed higher pollen viability and least reduction in fruit set, higher reduction in pollen germination and fruit weight per plant. This indicates the contribution of stigma was more in cv. Arka Vikas, which is evident from the increased fruit set even though the reduction in in vitro pollen germination was high. That can only happen when the stigma is efficient to fertilize with less efficient pollen; and abortion of fruits before reaching the maturity resulted in reduced fruit weight per plant. The same trend observed in cv. Arka Saurabh as well. In contrast to cv. Arka Vikas, IIHR 2195 showed reduction in pollen viability and fruit set, least reduction in vitro pollen germination and fruit weight per plant. This indicates the reduced capacity of stigma and pollen; and capability of plant to avoid the abortion of fruits leads to increased fruit weight per plant. The least reduction in fruit weight per plant is also an important trait under MET for the sustainable yield. Harvest index indicates the overall performance of genotypes, which consolidates the physiological, biochemical, morphological, growth responses and yield attributes under MTE. While considering all the four genotypes, cv. Arka Vikas showed higher harvest index. Increased fruit volume of cv. Arka Vikas under MTE, compensated reduction in fruit set, fruit weight per plant and number of fruits and increased harvest index.

5. Conclusion

In conclusion, four tomato genotypes showed wide variability in different vegetative, reproductive and yield traits under MTE. There was a positive correlation between pollen traits and fruit set, but there was no correlation found between pollen traits and final yield, which demonstrates the active involvement of stigma in reproductive success and yield. It is recommended that in future studies dealing with temperature stress, along with pollen traits, fruit set and yield, stigma receptivity should be included to draw the final conclusion with good relationships to identify the reasons for yield reduction. Further, in our earlier experiments with same four tomato genotypes, cv. Arka Vikas and IIHR 2195 showed better performance in biochemical and physiological screening; and the genetic advantages in morphological, physiological and biochemical traits can be attributed to the better harvest index and yield in current study. The systematic evaluation under controlled conditions in the present study further confirms the importance of cv. Arka Vikas and IIHR 2195 for their performance under MTE and inclusion in breeding programs for developing temperature tolerant cultivars for future climatic conditions by taking in consideration of studied traits.

6. Conflict of interest

The authors declare that there is no conflict of interest.

7. Acknowledgments

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